THE SUBEPIDERMAL NERVE PLEXUS AND GALVANOTROPISM OF THE EARTHWORM. (LUMBRICUS TERRESTRIS LINN.)

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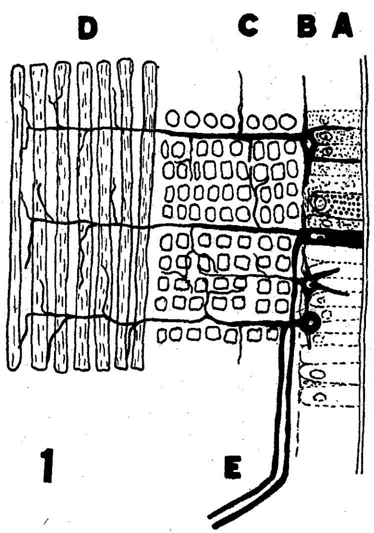
It is well known that the earthworm *Lumbricus terrestris* Linn. orients toward the cathode pole of direct electric current when the current is applied across a worm which is in water or on a moist surface. Moore and Kellogg (1916) explain this response as follows: "The constant current produces the effect described by increasing the tension of the longitudinal muscles on the cathode side of the worm, which results in this part being more strongly contracted than the anodal region." This is obviously a correct statement of the results, but it does not explain how these muscles at right angles to the direction of the current are made to contract on one side and not on the other.

Hyman and Bellamy (1923) in attempting to explain the same reaction say, "When Annelids are placed in a current the animals direct those parts positively charged internally toward the cathode and those parts negatively charged internally toward the anode." They do not explain, however, how a worm with a positive charge on the inside and a negative charge on the outside is made to bend toward the cathode. The reader is left to assume that there is an attraction between the negative charges of the cathode and the positive charges of the interior of the worm and vice versa.

Since the publications of the above in 1916 and 1923, respectively, Hess (1925) has described a subepidermal nerve plexus of the earthworm which might conceivably have some connection with the galvanotropic response. He has published a drawing of the subepidermal nerve plexus and the two sets of associated muscles. We have produced diagrammatically below (Figure 1) a similar drawing which shows the relations of the sensory cells to the muscles and to the central nervous system. This drawing, which is partly hypothetical, should be compared with Figures 6 and 7 of Hess (1925, p. 251 and p. 255).

To test the possible connection of the two, i. e., the subepidermal nerve plexus and the galvanotropic response, was the object of this investigation. The reasoning which led to the experiments to be described was as follows:

According to Lillie (1923, p. 276), "The stimulating action of a current is characteristically polar; i. e., the current produces its primary physiological effects chiefly at its regions of entrance and exit, and the effects at the two regions are typically opposite



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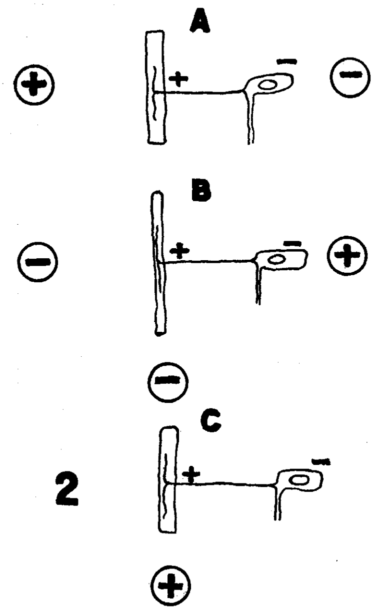

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FIG. 1. Diagram illustrating the probable relation of the sensory cells in the lateral body wall to the circular and longitudinal muscles. A, epithelial layer; B, subepidermal nerve cells; C, circular muscle layer; D, longitudinal muscle layer; E, sensory nerve fibers (cut) to the nerve cord.

FIG. 2. Diagram illustrating the arrangement of electrodes in relation to the subepidermal cells and muscles. The electrodes are shown inside circles. A, the current direction, which causes longitudinal muscle contraction; B, the current direction which causes longitudinal muscle relaxation; C, the current direction which stimulates the muscles directly causing contraction.

or antagonistic. Typically, when the current is made, it initiates excitation at the cathode, (i. e., where the positive stream of the stimulating circuit passes from the tissue to the applied electrode), and inhibits activity (at the same time depressing irritability) at the anode." The above statement of Lillie is the usual form of the "Law of Polar Stimulation."

From the above it should then follow that a negative pole applied to the skin surface of an earthworm and a positive pole applied on the opposite (muscle) side should result in the stimulation of the subepidermal neurons and contraction of the circular and longitudinal muscles, provided that all traces of the ventral cord are removed. The reverse arrangement, i. e., the positive pole on the skin side and the negative pole on the muscle side should inhibit the stimulation of the neurons and relax the circular and longitudinal muscles. (See Figure 2.)

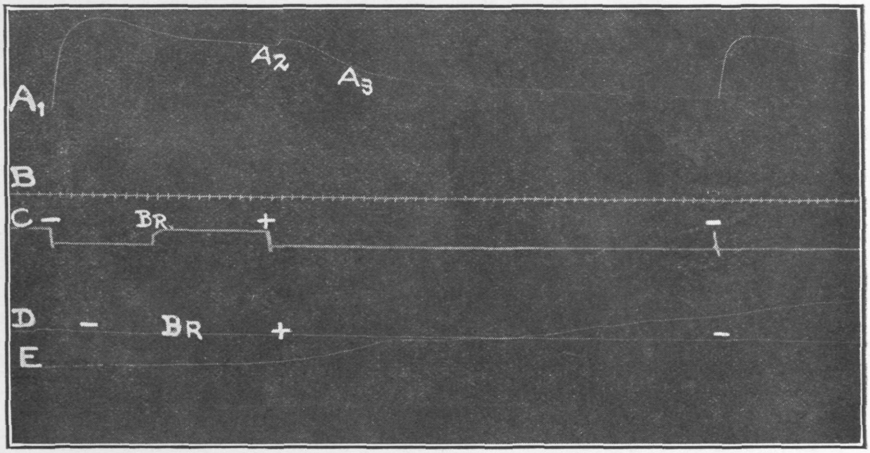

FIG. 3. Kymograph tracings which show the muscle responses under different conditions. A_1, A_2, A_3, tracing of muscle lever. The upward curve indicates contraction of the longitudinal muscles; B, time scale in seconds; C, tracing of magnet lever showing current and direction of current; D, tracing of muscle lever using narcotized tissue and direction of current; E, tracing of narcotized muscle when the current is passed lengthwise through the muscle.

APPARATUS AND METHODS.

From an earthworm that has been previously cooled in ice water a strip of lateral body wall about one and a half inches long and a quarter of an inch wide was removed. This was examined to be sure that it contained no trace of the ventral nerve cord. One end of the muscle was attached to a lever with a writing point and the other end to the bottom of a wax-lined dissecting dish. The writing point was placed against a smoked paper on a kymograph drum. Below this point was arranged a time lever and a lever connected to the reversible switch. (Figure 3, B and C.) On each side of the living strip of body wall was placed a screen wire electrode so arranged that one electrode was parallel to the skin side and another was parallel to the muscle side. By means of a reversible switch the screen electrodes could be charged as desired. The current being derived from five dry batteries in series. Ice water was used as a conducting medium between the electrodes and the living strip of tissue. As soon as the current was made across the strip of tissue the lever registered the break or make of the current and the living strip either contracted or relaxed, making the records on the drum.

EXPERIMENTS.

Experiment 1.

In this experiment the electrodes were so arranged that the negative was on the skin side and the positive on the muscle side. The current was made registering on the drum (C—), at the same time the lever attached to the strip of tissue also registered at (A_1) showing a sudden contraction of the strip. Time is recorded in seconds at (B).

The result of the make of the current as described before is a contraction of the muscles as is shown on the graph. The current was kept going for nine and one-half seconds. The contraction of the muscle is shown by the rise of the line at (A_1). The current was then broken at the point marked Br. on the line (C). The lever attached to the tissue showed the gradual relaxation of the tissue for eleven seconds. Then the current was reversed at the point marked + on line C on the graph. The plus sign indicating that the positive electrode was at the skin side. Immediately the lever attached to the tissue showed a slight contraction at A_2 followed by a sudden relaxation. The current was kept on for forty-four seconds, thereby gradually lowering the curve (A_3) almost to the base line. Then the current was reversed again at the point marked — on curve (C) on the graph. Again the same result was registered as at (A_1).

Experiment 2.

The same strip of tissue is now allowed to soak in a very dilute solution of nicotine for four minutes. It is then taken out and attached again as in Experiment 1. The current is made at point marked — on curve (D). The current is kept on for eight seconds. The current is then broken at the point marked Br. on curve (D) and the circuit is kept open for eight seconds. Then the current is on in reversed direction at the point marked + on the curve (D) and is kept that way for one minute. In this experiment one will notice that the curve made by the lever attached to the tissue line D was a straight line; indicating that the current had no effect whatsoever on the muscle tissue, which in the previous experiment gave clear cut results.

Experiment 3.

To the two ends of this same strip of tissue are now attached two wires in such a way that the same current can be sent through the muscle parallel to the direction of the fibres. The curve made by the lever attached to the muscle tissue in this case is the last one on the graph (E). The current was kept on for a minute and a half. The curve made by the lever in this case goes completely over the curve (D) made when the tissue was stimulated at right angles to the surface of the tissue (Experiment 2).

The results of experiments 1, 2, and 3 as detailed above are typical of five series which were carried out.

DISCUSSION OF RESULTS.

It was shown in Experiment 1 that the muscles contracted when the current was so arranged that the negative electrode was on the skin side and the positive electrode was on the muscle side, and that the muscles relaxed when the polarity of the current was reversed. Experiment 2 demonstrated the fact that when the strip of tissue which was treated with nicotine (thereby eliminating all nervous action) was at right angles to the current there was no reaction at all to the current. Experiment 3 showed that the muscles were still alive, since, when the current was run through the tissue lengthwise the muscles contracted.

This sequence of events shows by elimination that the contraction of the muscles in Experiment 1 was due to the stimulation of the subepidermal neurons and that these neurons were polarized in such a way that a reversal of the current caused not only a cessation of muscle stimulation but an active relaxation or loss of tone.

From the above it is quite clear that the neurons of the subepidermal nerve plexus control the longitudinal muscles of the body wall of the earthworm directly and that they are electrically polarized at right angles to the surface.

The usual electrotactic response of a worm which is immersed in water can now be explained on a cause and effect basis. The longitudinal muscles on the side toward the cathode are stimulated because the polarity of the motor cells in the subepidermal nerve plexus is increased. At the same time the muscles on the side toward the anode are relaxed because the normal polarity of the motor nerve cells is decreased or possibly reversed. The two processes acting at the same time on opposite sides of the worm cause the worm to bend toward the cathode.

We are making no mention at this time of the fact that a normal worm crawls toward the cathode. The mechanism which controls this crawling is more complicated and evidently is not in any large way due to the action of the subepidermal nerve plexus.

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The Broad Field of Zoology.

This introductory zoology text is somewhat unique in that it is based on the author's belief that students should approach their study of zoology from the things with which they are familiar, and thus proceed to the aspects which are less familiar to them. With this very commendable basis, the book is built around the rat as an example of the mammals. System by system the rat is studied, with each chapter broadening out at the end into a discussion of that system in the vertebrates in general. Following reproduction are taken up embryology and heredity; following the skeletal system, locomotion; following the nervous system, animal behavior, etc. The book ends with a section on philosophical zoology, including distributional zoology, paleontology, and evolution. The impression given by the book is one of clear, well-rounded, authentic subject-matter, uniquely and practically arranged. Numerous original illustrations add considerably to the text. This book is intended as a companion volume in the elementary course to the author's earlier volume on Economic Zoology.—L. H. S.

An Introduction to Zoology, by Z. P. Metcalf. xix + 425 pp. Springfield, Ill., Charles C. Thomas, 1932.